

PHYLOGENY AND EVOLUTIONARY ECOLOGY OF MODERN SEADUCKS (ANATIDAE: MERGINI)¹

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Abstract. Phylogenetic relationships of modern seaducks (Mergini) were investigated using a cladistic analysis of 137 morphological characters. The analysis produced a single tree (consistency index = 0.692, excluding autapomorphies) with complete resolution of the relationships among the 25 taxa recognized. Phylogenetic inferences include: (1) the eiders (*Polysticta* and *Somateria*) constitute a monophyletic group and are the sister-group of other Mergini; (2) the remaining generic groups of Mergini, sequenced in order of increasingly close relationship, are *Histrionicus*, *Melanitta* + *Camptorhynchus*, *Clangula*, *Bucephala* + *Mergellus*, *Lophodytes*, and *Mergus*; (3) *Somateria* is monophyletic with *S. fischeri* the sister-group of its congeners; (4) the black scoters (*Melanitta nigra*-group) are the sister-group of other scoters; (5) the Bufflehead (*Bucephala albeola*) is the sister-group of the goldeneyes (*B. clangula* and *B. islandica*); and (6) relationships among mergansers are as presented by Livezey (1989). Bootstrapping revealed that the placement of the Smew as the sister-group of the goldeneyes is only weakly supported, and ancillary analyses revealed that this placement is only one step shorter than its reduction to a trichotomy with the goldeneyes and mergansers (including *Lophodytes*). A phylogenetic classification of modern seaducks is presented. The Harlequin Duck (*H. histrionicus*), Long-tailed Duck (*Clangula hyemalis*), and Steller's Eider (*Polysticta stelleri*) are highly autapomorphic. Evolutionary patterns of selected ecomorphological characteristics—including body mass, sexual size dimorphism, clutch size, relative clutch mass, nest site, diet, diving method, formation of crèches, and biogeography—are examined with respect to the phylogenetic hypothesis.

Key words: *Anatidae*; *biogeography*; *comparative ecology*; *Mergini*; *morphology*; *phylogeny*; *plumage*; *seaducks*; *waterfowl*.

INTRODUCTION

Seaducks (Anatidae: Mergini) comprise a monophyletic group of diving ducks largely limited in distribution to the northern hemisphere (Livezey 1986). All but one species of Mergini spend at least part of the year on saltwater (Phillips 1925, 1926; Delacour 1959; Johnsgard 1978), and the group is perhaps best known for the conspicuous, large, wintering flocks of several species of seaduck in Europe and North America. Two species of Mergini have become extinct during historical times, the Labrador Duck (*Camptorhynchus labradorius*) and Auckland Islands Merganser (*Mergus australis*), and several other species have undergone significant declines (King 1981, Collier et al. 1992, Wilson Ornithological Society Resolutions Committee 1993). Fossil specimens of Mergini are mostly of Pleistocene age or younger (Brodkorb 1964, Howard 1964), although fossils from as early as the Miocene have been assigned to the tribe (Alvarez and Olson 1978).

Systematists generally have agreed upon the composition of the group (Delacour and Mayr 1945; Boetticher 1942, 1952; Johnsgard 1961a, 1961b; Livezey 1986). Exceptions to this consensus were the failure to segregate the Mergini from other diving ducks (Salvadori 1895; Phillips 1925, 1926; Peters 1931) and the tribal separation of the eiders from other Mergini (Humphrey 1955, 1958a; Delacour 1959; Cramp and Simmons 1977). Earlier morphological studies provide differing, fragmentary, and often phenetic assessments of phylogeny within the tribe (Delacour and Mayr 1945; Verheyen 1953; Delacour 1959; Johnsgard 1961a–1961c, 1964, 1965, 1978, 1979; Woolfenden 1961). Livezey (1986) presented a genus-level phylogenetic analysis of modern Anseriformes based largely on osteological comparisons, but species-level analyses were not attempted. Livezey (1989) presented a preliminary, species-level phylogenetic analysis of the mergansers using morphological characters.

Molecular studies of the phylogeny of seaducks have been similarly limited. Jacob and Glaser

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(1975) and Jacob (1982) found that composition of integumental lipids confirmed a moderate distance between the Common Eider (*Somateria mollissima*) and several other genera of Mergini. Brush (1976) found a clear distinction between the eiders and other Mergini using feather proteins, but was unable to make any finer resolutions within the tribe. Patton and Avise (1985), using electrophoresis of 13 proteins, reported a moderately large genetic distance between two species of *Bucephala* and the two other Mergini sampled (*Melanitta* and *Clangula*). Recent comparisons of Anseriformes using DNA hybridization included only a single representative of the Mergini (*Melanitta*) and therefore provided no insights into relationships within the tribe (Sibley and Ahlquist 1990, Sibley and Monroe 1990). Similarly, comparisons using DNA hybridization by Madsen et al. (1988) included only one species of Mergini, the Hooded Merganser (*Lophodytes cucullatus*).

This paper presents a phylogenetic analysis of modern Mergini using characters of the skeleton, trachea, natal plumage, and definitive plumages. An exposition of the phylogenetic hypothesis is followed by a comparative analysis of selected characteristics of life history and biogeography based on the proposed phylogeny, and a phylogenetic classification is proposed.

MATERIALS AND METHODS

TAXONOMY

For purposes of this analysis, I recognized 25 species-level taxa in the Mergini, which followed conventional taxonomy (e.g., Johnsgard 1979) with three exceptions. These 25 operational units were the result of merging, for purposes of analysis, subspecies within polytypic species that were identical for all characters coded. These practical delimitations are broadly consistent with those prescribed by application of the phylogenetic species concept (Cracraft 1983, 1988; McKittrick and Zink 1988). The Common Eider complex (*Somateria mollissima*-gp.) was partitioned into four operational units: (1) *mollissima* of northwestern Europe, including comparatively small *faeroensis* and provisionally *islandica*; (2) *borealis* of the arctic North Atlantic; (3) *dresseri* of Atlantic North America, including *sedentaria*; and (4) *v-nigrum* of the North Pacific. The Black Scoter complex (*Melanitta nigra*-gp.) was divided into two allopatric hemispheric forms—Pa-

learctic *M. nigra* and Nearctic *M. americana*. Similarly, two species were recognized within the White-winged Scoter complex (*Melanitta fusca*-gp.)—Palearctic *M. fusca* and largely Nearctic *M. deglandi* (including *stejnegeri*).

SPECIMENS AND MATERIAL EXAMINED

With the exception of the extinct Labrador Duck, for which only a few appendicular elements were available for study (Humphrey and Butsch 1958, Zusi and Bentz 1978), skeletal specimens of all species of Mergini were examined for this analysis. Many of the osteological characters used here were adapted from the ordinal analysis by Livezey (1986), a number of which were illustrated by Shufeldt (1888), Schiøler (1926), Woolfenden (1961), and Möller (1969a, 1969b). Osteological nomenclature follows Baumel (1979), as revised by Baumel and Witmer (1993). Tracheae of males of all species but the Labrador Duck and Brazilian Merganser (*Mergus octose-taceus*) also were studied directly; a few characters of the former were taken from nineteenth-century descriptions (see Humphrey and Butsch 1958), and characters of the latter were coded using illustrations prepared by Humphrey (1955). Additional information on tracheal anatomy was taken from earlier studies (Latham 1798; Schiøler 1926; Beard 1951; Humphrey 1955, 1958a; Johnsgard 1961b, 1962; Humphrey and Clark 1964).

Natal plumages were compared using study skins of downy young for all species except the Labrador Duck (for which even historical descriptions are not available) and the Brazilian Merganser (codings for which were based on illustrations and descriptions in Delacour 1959 and photographs in Bartmann 1988). Characteristics of natal plumages also were confirmed using the descriptions and illustrations given by Schiøler (1926), Phillips (1925, 1926), Delacour (1959, 1964), Palmer (1976), and Nelson (1993). Several of the plumage characters described by Livezey (1989) for natal and adult *Mergus* were excluded or modified to permit consistent, more clearly defined states for coding throughout the tribe. Characters of definitive plumages of sea-ducks were defined through comparison of series of study skins of both sexes of each taxon, with anatomical details (especially colors of soft parts) confirmed through published descriptions of states in live or freshly collected birds (Dwight 1914; Miller 1916, 1926; Taverner 1919; Schiø-

er 1926; Kagelmann 1951; Delacour 1959; Partridge 1956; Humphrey and Butsch 1958; Johnsgard 1960a, 1978; Palmer 1976; Lucas 1979; Madge and Burn 1988; Garner 1989; Livezey 1989).

Outgroups were selected on the basis of intergeneric relationships inferred by Livezey (1986, 1991) and included several species of Anatini (sensu Livezey 1991; e.g., *Cairina moschata*, *Mareca americana*, *Anas platyrhynchos*), as well as basal Oxyurini (e.g., *Heteronetta atricapilla*) and Aythyini (e.g., *Marmaronetta*, *Netta*). Polarities of each character, based on distributions of states among outgroups, were used to construct a "hypothetical ancestor" for rooting the tree(s). Relationships among outgroups remain poorly resolved (Livezey 1986, 1991), therefore the method of "successive outgroups" could not be employed (Maddison et al. 1984). Study skins of adults, and samples of skeletons, tracheae, and downy young were used to establish character polarities.

A number of generalized physical and functional attributes vary among the Mergini in ways that defied subdivision into discrete, homologous character states. For example, an increase in body mass in one lineage might result from enlargement of the pelvic musculature whereas an equal increase in mass in another lineage might reflect a generalized increase in bulk throughout the body. Consequently, such variables were not included as characters in phylogenetic inference, but instead were mapped *a posteriori* onto a tree inferred using other data (Appendix 1). None of these mapped attributes are known for the Labrador Duck, and many also remain undetermined for the Auckland Islands and Chinese Mergansers. These ancillary data—including body mass, clutch size, egg size, nesting habits, diet, and diving behavior—were taken from the literature (Townsend 1909; Kelso 1922; Brooks 1945; Humphrey 1957, 1958b; Delacour 1959; Schönwetter 1961; Weller 1964a–1964d; Kear 1970; Raikow 1973; Bellrose 1976; Palmer 1976; Cramp and Simmons 1977; Snell 1985; Eadie et al. 1988; Madge and Burn 1988; Rohwer 1988; Kehoe 1989; Livezey 1989; Rohwer and Freeman 1989; McNeil et al. 1992; Dunning 1993). Mean body masses of species were estimated by the unweighted mean of the mean masses for adults of the two sexes separately. "Sexual size dimorphism" was measured by the ratio of the mean body mass of males divided by the mean

body mass of females. "Relative clutch mass" was defined as the product of mean clutch size and mean egg mass divided by the mean body mass of adult females. Data on body mass were not available for the Labrador Duck, Auckland Islands Merganser, or Brazilian Merganser; estimates of body mass for the last two species were taken from Livezey (1989). Such attributes were difficult to assign to one of two classes in some species, e.g., preferred nest site being "ground" versus "cavity" for the Harlequin Duck or frequency of nest parasitism in several species. Therefore in these cases codings represent the "typical" or modal state for each species.

ANALYSIS OF CHARACTERS

A total of 137 morphological characters were identified that defined or varied within the Mergini: 20 skeletal characters (17 modified from those of Livezey 1986), eight tracheal characters, 17 characters of natal plumage, and 92 characters of the plumage and soft parts of adults (Appendix 1). Each character comprised a primitive (plesiomorphic) state and one or more derived (apomorphic) states. All species of Mergini (the ingroup) were coded for each character, specimens permitting; species for which a character state could not be ascertained were assigned a missing-datum code for that character. These character-state codes compose a 25×137 data matrix (Appendix 2). Characters having more than one derived state were considered unordered unless a logical, consistent ordination by count, degree, or relative extent was evident. Characters in which the derived state(s) were hypothesized to occur in terminal lineages (autapomorphies) were included in the analysis because of the pervasive influence such differences have had on traditional classification. Moreover, inclusion of autapomorphies confirms monophyly of terminal taxa, permits estimates of evolutionary divergence, and explicitly accounts for phenetic differences among species within the phylogenetic tree. The consistency indices for all characters were compared to assess the phylogenetic utility of characters used in this analysis and in those of other tribes of Anseriformes (Livezey 1991, unpubl. manuscripts).

DERIVATION OF TREES

The fundamentals of phylogenetic analysis are described by Wiley (1981), and similar analyses of morphological data of Anseriformes were re-

ported by Livezey (1986, 1989, 1991). Trees were constructed using the phylogenetic software PAUP 3.1 (Swofford 1993); supplementary topological analyses, *a posteriori* character mappings, and printing of trees were performed on MacClade 3.01 (Maddison and Maddison 1992). Both programs were implemented on a Macintosh Quadra 800. I used heuristic algorithms (global branch swapping) to find the shortest tree(s), with MAXTREES set to 1,000 and the MULPARS options in effect. Results were unchanged if the "random" sequence option for addition of taxa was used instead of the default option of "simple" addition. The character-state optimization used was accelerated transformation (ACCTRAN); employment of delayed transformation (DELTRAN) did not affect the solution set. Bootstrapping of characters was used to assess the relative stability of the resultant branch patterns (Felsenstein 1985). This procedure—using heuristic methods, simple addition of taxa, five trees held at each step, the MULPARS option in effect, and trees held in memory (MAXTREES) of 1,000—was used to generate 100 topological replications. Stability of branches within the final tree was summarized by a 50% majority-rule consensus tree of these 100 replicates. A strict interpretation of the resultant percentages as statistical confidence levels is not recommended, given the sampling assumptions required for such inference (Sanderson 1989).

PHYLOGENETIC CLASSIFICATION

The resultant phylogenetic tree(s) formed the basis for a Linnean classification that maximally reflects the relationships inferred for the ingroup. Unconventional taxonomic ranks (subtribes, supergenera, and subgenera) were based on senior taxa of appropriate rank, in part based on the classifications of Boetticher (1942, 1952) and the synonymies of Phillips (1925, 1926), Brodkorb (1964), and Wolters (1976).

RESULTS

PHYLOGENETIC TREE

A single most-parsimonious tree was found (Fig. 1). The tree was completely dichotomous, had a length of 223, a consistency index (excluding uninformative characters) of 0.692, a retention index of 0.894, and a rescaled consistency index of 0.681. The eiders (*Polysticta* and *Somateria*) were found to be monophyletic and these two genera constitute the sister-group of all other

seaducks. Within the latter, the Harlequin Duck (*Histrionicus*) is the sister-group of the remaining genera. Two major clades are defined within the genera of Mergini exclusive of the eiders and the Harlequin Duck: (1) a clade in which the Labrador Duck is the sister-group of the scoters (*Melanitta*); and (2) a clade in which the Long-tailed Duck (*Clangula*) is the sister-group of the goldeneyes (*Bucephala*), Smew (*Mergellus*), and mergansers (*Lophodytes* and *Mergus*).

Steller's Eider (*Polysticta*) was found to be the sister-group of the greater eiders (*Somateria*). Within the latter, the Spectacled Eider (*S. fischeri*) is the sister-group of the King Eider (*S. spectabilis*) and the Common Eider complex (*S. mollissima*-gp.). The *mollissima* complex is resolved, in order of increasingly close relationship, as the Pacific Eider (*v-nigrum*), Northern Eider (*borealis*), Canada Eider (*dresseri*) and European Eider (*mollissima*). Within the scoter clade, the black scoters (*M. nigra* and *M. americana*) compose the sister-group of the other scoters; in the latter group, the Surf Scoter (*M. perspicillata*) and the sister-species of white-winged scoters (*M. fusca* and *M. deglandi*). This analysis resolves the Smew to be the sister-group of the goldeneyes; within the latter, the Bufflehead (*B. albeola*) is the sister-group of the typical goldeneyes (*B. clangula* and *B. islandica*). Among the mergansers, the Hooded Merganser (*Lophodytes*) is the sister-group of other mergansers (Fig. 1). Within *Mergus*, a basal grade of the southern-hemispheric species (*M. australis* and *M. octosetaceus*) subtends a terminal clade in which the Common Merganser (*M. merganser*) is the sister-group of the Red-breasted (*M. serrator*) and Chinese Mergansers (*M. squamatus*).

BRANCH LENGTHS AND STABILITY

Stability of topology. One measure of supporting evidence for each grouping is the number of synapomorphies that define its basal stem (Fig. 1). Monophyly of the tribe is supported by 13 synapomorphies, of which 11 are unambiguous (i.e., only one distribution of states permitted in the shortest topology) and seven had unit consistency (CI = 1.0). Comparatively great support is given to the goldeneye-Smew-merganser clade (17 synapomorphies, 9 unambiguous) and *Somateria* (13, 10), whereas only three character changes (all unambiguous) unite the Long-tailed Duck with the goldeneye-merganser clade.

The percentage of bootstrapped replications of

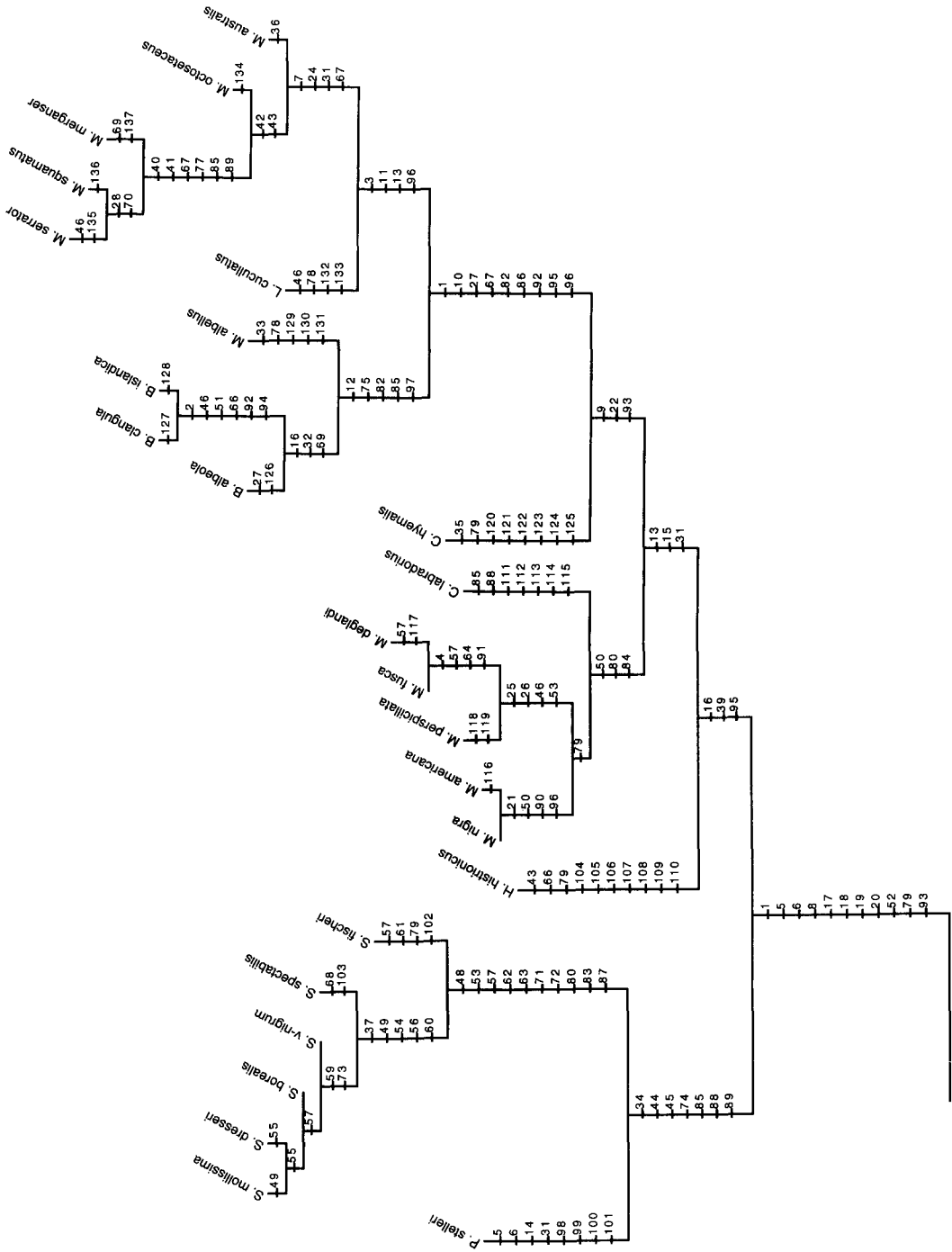


FIGURE 1. Most-parsimonious phylogenetic tree (phylogram) for the Mergini based on 137 morphological characters. Characters undergoing changes in state are indicated by number on each branch (see Appendix 1 for character descriptions, Appendix 2 for matrix of character states).

the tree that retain a given branch offers an alternative assessment of topological stability (Fig. 2). All branches in the final tree (Fig. 1) except the one uniting the Smew with the goldeneyes were preserved in a majority of the replicate topologies. Other branches varied in the percentages of the topologies in which they were retained (Fig. 2). Nine branches were preserved in over 90% of the replications, including those uniting: (1) the eiders (*Polysticta* and *Somateria*); (2) the genus *Somateria*; (3) the three subgroups within the scoters; and (4) the goldeneyes, Smew, and mergansers. Comparatively weak support was indicated for several other branches, including those defining: (1) the members of the Common Eider complex (61% of replications); (2) the Long-tailed Duck with the goldeneye-Smew-merganser clade (58%); (3) the Mergini exclusive of the eiders (65%); and (4) the Mergini exclusive of the eiders and Harlequin Duck (68%). Instability within the Common Eider complex partly reflects the (modal) distribution of the black gular chevron (character 62) within the group; the polarity of this character in the shortest tree (Fig. 1) indicates that its infrequent appearance in *Somateria* exclusive of *spectabilis* and *v-nigrum* may be atavistic. The bootstrapped percentages and counts of synapomorphies produced somewhat different assessments of support for several other branches in the tree, in part because several of the included synapomorphies were of low consistency. For example, support for the branches within the scoters (five synapomorphies each, 93–99% of replicates) contrasts with that for the branch uniting the Smew with the goldeneyes (five synapomorphies, <50% of replicates).

Monophyly of species and autapomorphic divergence. Four terminal branches lacked autapomorphies (Fig. 1), therefore monophyly of the corresponding taxa was not demonstrated. These taxa comprise two members of the *Somateria mollissima* complex (*borealis* and *v-nigrum*), and the nominate forms of the white-winged and black scoter complexes (*Melanitta fusca* and *M. nigra*). These zero-length terminal branches do not indicate that the affected taxa should be merged with their sister-species, because the taxa are distinguishable from all others by combinations of characters in the tree. However, further character analysis is needed to determine whether these taxa are natural groups or define paraphyletic or polyphyletic groups.

Several species were characterized by pro-

nounced autapomorphic divergence (i.e., character changes in terminal lineages), much of which involved unique aspects of plumage patterns of adults, and has tended to obscure their phylogenetic relationships when classified by phenetic criteria. These divergent species are the Harlequin Duck (11 autapomorphies, 7 unique for the entire tribe), Long-tailed Duck (10, 7), Steller's Eider (8, 5), Labrador Duck (8, 5), and Smew (8, 3). Several of these terminal character changes are not unique within the tribe and hence are of lower consistency, and in several of the foregoing species (especially the Harlequin Duck, Long-tailed Duck, and Smew) contribute to the instability of their placements in the tree.

CONSISTENCY OF CHARACTERS

The four major character groups had similar average consistency indices (CI): skeletal (0.87 total, 0.86 excluding unique autapomorphies), tracheal (0.88, 0.88), natal (0.79, 0.75), and definitive integument (0.89, 0.80). Although a majority of characters in each character set had consistency indices of 1.0, there were characters in each set showing one or more reversals or convergences. Skeletal characters having comparatively low CIs involved the processus supraorbitalis (character 1) and the foramen pneumaticum sterni (character 5). Two characters of the trachea—relative cranial prominence of the bulla syringealis (character 23) and presence of a bulbus trachealis (character 27)—also had low CIs. Three characters of the natal plumage had exceptionally low CIs: presence of pale dorsal spotting (character 30), presence of a dark pectoral band (character 31), and ventral ground color (character 34). Finally, a small minority of the characters of the definitive integument had low consistencies, with convergences playing a slightly larger role than reversals in the added evolutionary steps. The latter included ground color of the bill (character 48), blackish lateral barring (character 81), ground color of lesser dorsal wing coverts (character 85), and color of axillaries (character 88).

ECOMORPHOLOGICAL COROLLARIES

Body mass. Body mass and several related attributes showed strong phylogenetic patterns among the Mergini (Fig. 3). There is a strong trend toward increased mass in the eiders (especially *Somateria*), with lesser trends toward increased bulk in the scoters (especially *M. fusca* and *M. deglandi*) and within the mergansers (a

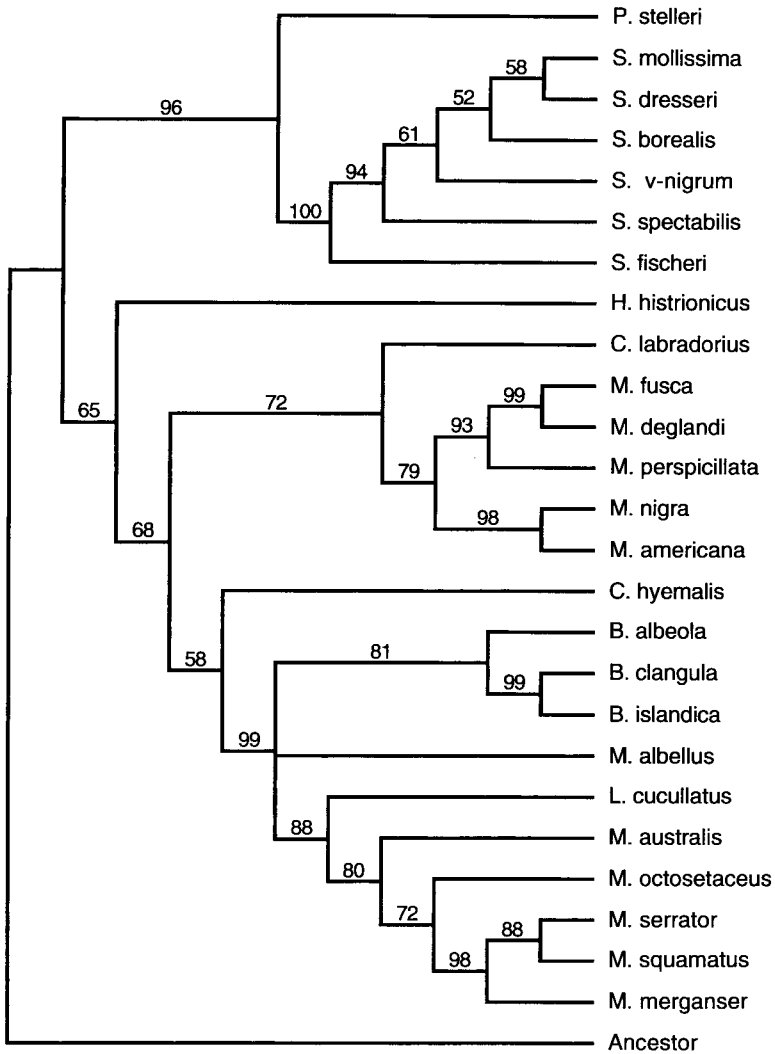


FIGURE 2. Fifty-percent majority-rule consensus tree of 100 bootstrapped replications of the shortest phylogenetic tree of the Mergini (Fig. 1). Percentages of replications in which each branch was conserved are indicated.

local extreme being attained in *Mergus merganser*). Sexual size dimorphism (Fig. 3) also showed very strong phylogenetic patterning in the Mergini, but was not associated with patterns in mean body mass (Fig. 3). Independent increases in sexual size dimorphism (Fig. 3) are indicated in the Harlequin Duck and the white-winged scoter complex, and a strong trend toward increased dimorphism is evident among the goldeneyes, Smew, and the mergansers (the highest value for the tribe being in the goldeneyes). Sexual dichromatism is primitive for the tribe, but evidently underwent independent reversals in the

two southern-hemisphere mergansers (not figured, see Appendices 1, 2).

Reproductive parameters. Mean egg mass closely followed interspecific patterns in body mass. Phylogenetic patterns in clutch size, however, were complex and showed negligible correspondence with trends in body mass. The tree indicates that the tribe underwent an initial modest decrease in clutch size, followed by a further decrease in *Somateria* and subsequent increases in the white-winged scoters and independently in the goldeneyes and mergansers (Fig. 3). Relative clutch mass, perhaps the best single indi-

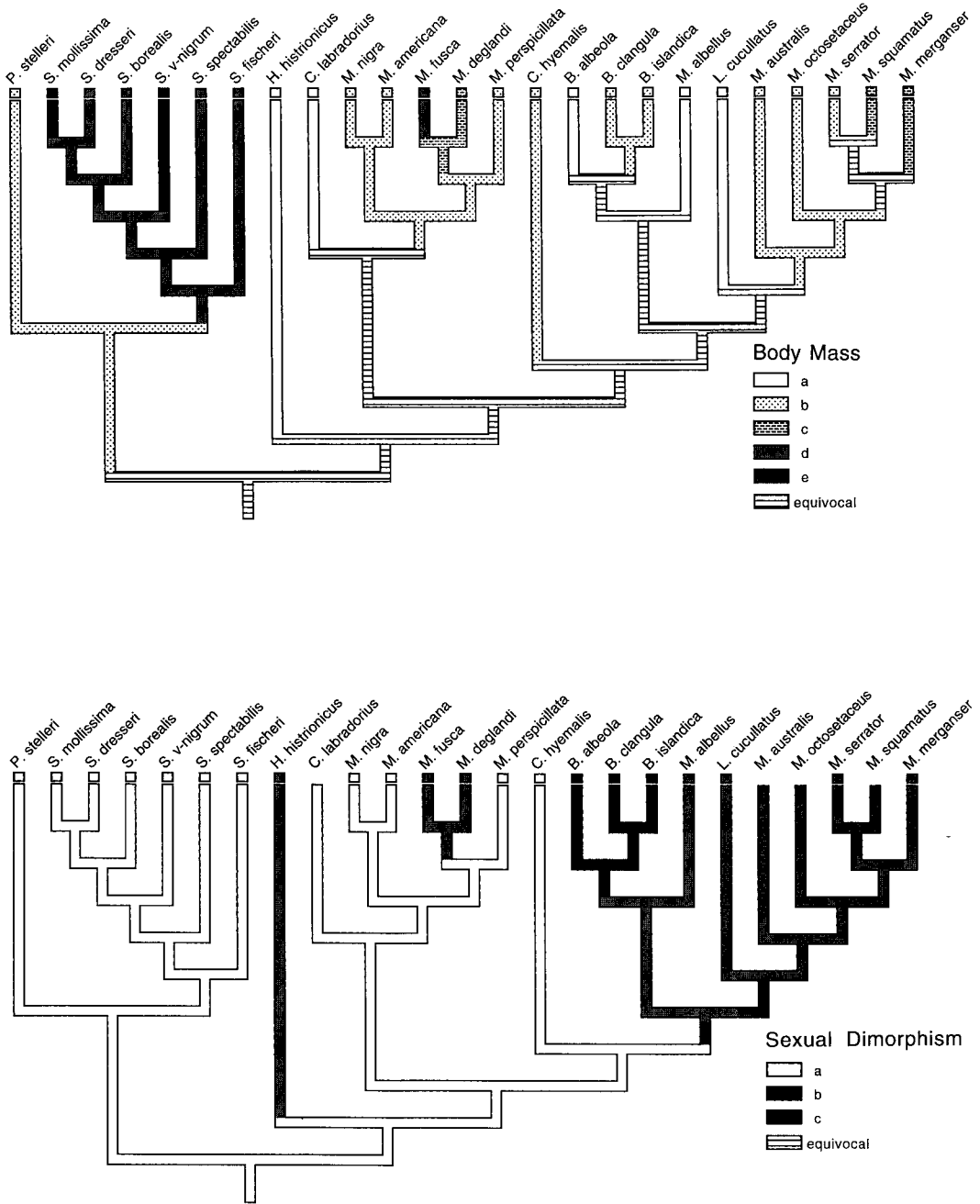


FIGURE 3. Mappings of selected characteristics on phylogeny of the Mergini: mean body mass, sexual size dimorphism, mean clutch size, and relative clutch mass. States are indicated by shading patterns on branches (see adjacent keys). See Appendix 1 for character descriptions (attributes A, B, D, and I, respectively), Appendix 2 for data matrix.

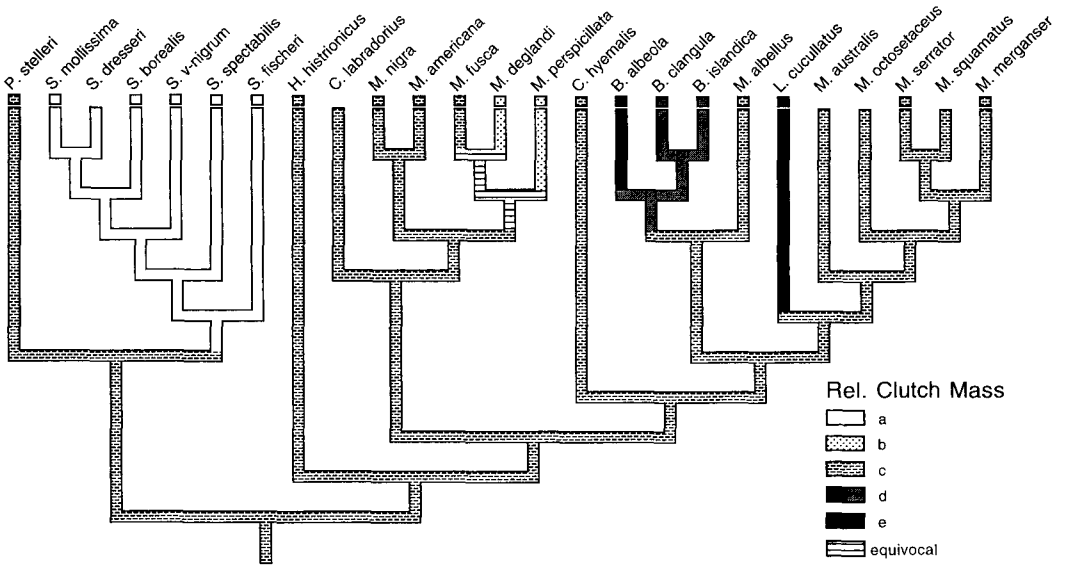
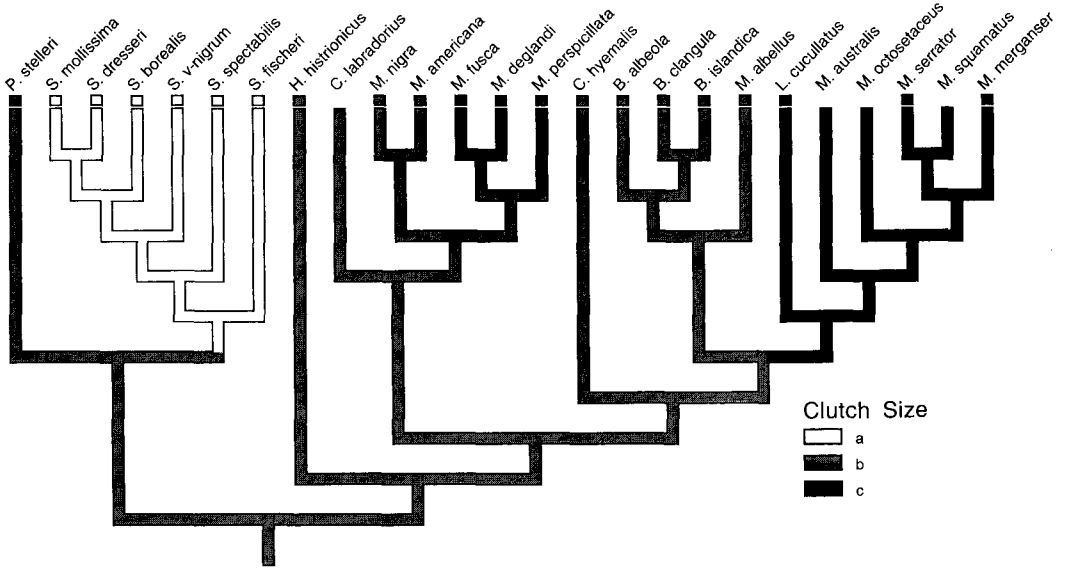


FIGURE 3. Continued.

cator of relative reproductive investment prior to hatching, is comparatively high in the Mergini generally, but evidently underwent a significant decline in *Somateria* and independent increases in the goldeneyes and the Hooded Merganser (Fig. 3). Age of sexual maturity is two or more years in the Mergini, apparently a derived condition shared by all members of the tribe (not figured, see Appendices 1, 2).

Primary selection of terrestrial nest sites is primitive in the Mergini, characterizing all but the goldeneyes, Smew, and mergansers; the latter share a derived preference for nest cavities. A pronounced preference for semicolonial nesting is shared by *Somateria*, as is the frequent formation of crèches. Intraspecific nest parasitism occurs in all Mergini at least infrequently, but available data mapped on the phylogeny of the tribe indicates that significant increases in frequency have evolved in three groups independently: the Common Eider complex, the goldeneyes, and the mergansers. Interspecific nest parasitism is less well documented among the Mergini, but these data indicate that increases in this behavior have evolved in the two large goldeneyes (*Bucephala clangula* and *B. islandica*) and independently in the Hooded Merganser (Appendices 1, 2).

Habitat, locomotion, and diet. Although most species of Mergini occur at times on both fresh and salt water, a preference for one or the other feeding habitat generally characterizes each species, at least during nesting and brood-rearing. The presumed primitive preference is for freshwater, a condition retained by most members of the tribe (not figured, see Appendices 1, 2). Independent shifts to approximately equal use of the two habitats are hypothesized for the white-winged scoters and the Long-tailed Duck, and a shift to coastal breeding areas is evident within the eiders. Method of diving, which involves strokes of both wings and feet in dabbling ducks and most Mergini, evidently underwent a specialization to feet-only diving in the ancestor of the goldeneyes, Smew, and mergansers. For the mergansers and the Smew, this change in locomotor method evidently was coincident with a shift to piscivory (Appendices 1, 2).

DISCUSSION

PHYLOGENETIC RELATIONSHIPS AND CLASSIFICATION

Natural classification of Mergini. The phylogenetic hypothesis proposed here is consistent with

a Linnean classification including the following classificatory points (Appendix 3): (1) subtribal separation of the eiders from other seaducks; and (2) three supergenera within the latter subtribe. The position of the Smew remains only marginally supported, although the preferred hypothesis is a sister-group status with the goldeneyes (Fig. 1); accordingly, I retain the taxon *Mergellus* as a monotypic genus. Recognition of the following taxa at species level is recommended (see Appendix 3 for subspecific assignments): Pacific Eider (*Somateria v-nigrum*); White-winged Scoter (*Melanitta deglandi*); and American Black Scoter (*M. americana*). The isolation of the Pacific Eider presumably was associated with divergence in a glacial littoral refugium (Rand 1948, Ploeger 1968). The other three taxa in the *Somateria mollissima* complex analyzed here will require further character analysis throughout their respective distributional ranges (including a quantitative reassessment of the bill characters coded here) before formal consideration of species status is warranted. Preliminary study of the fossil genus *Chendytes* indicates that these flightless ducks of the Pacific coast of North America were most closely related to the eiders (Livezey 1993).

Comparison with other authorities. The order of genera proposed in the classic taxonomic arrangements by Delacour and Mayr (1945) agrees with that inferred here except that: (1) Steller's Eider was included within *Somateria*; (2) the Harlequin Duck was placed after the Labrador Duck and scoters instead of immediately after the eiders; and (3) the Smew was placed in *Mergus* as its first member. The sequence used by Delacour (1959) was identical except that the eiders were segregated in a separate tribe (*Somateriini*) and separated in tribal sequence from other seaducks by the pochards (*Aythiini*) and "perching ducks" (*Cairinini*). Johnsgard (1960a) largely concurred with the arrangement by Delacour (1959), except that he recommended: (1) that the eiders be included with other seaducks; (2) that *Somateria* precede *Polysticta*; (3) that the Labrador Duck immediately follow the eiders; and (4) that the Long-tailed Duck precede the scoters.

Johnsgard (1961a: 82) depicted a tree of "evolutionary relationships" in the Mergini based largely on behavioral data. It differed from the present hypothesis (Fig. 1) in several ways: (1) Steller's Eider was shown as the sister-group of the Mergini exclusive of *Somateria*; (2) the Labrador Duck was tentatively placed between the

eiders and the Harlequin Duck; (3) the Long-tailed Duck was considered to be less closely related to the goldeneyes and mergansers than the scoters; (4) the Smew was considered the sister-group of the mergansers exclusive of the Hooded Merganser; and (5) the Common and Chinese Mergansers were considered sister-species, with the Auckland Islands Merganser tentatively placed as their sister-group. Johnsgard (1961c, 1964) provided additional arguments in support of the taxonomic positions of the eiders and Hooded Merganser. Taxonomic sequences used subsequently by Johnsgard (1978, 1979) were identical with his earlier (1961a) arrangement, except that Johnsgard (1979) listed the Smew before the Hooded Merganser.

Manipulation of branches revealed that the hypothesis of paraphyly of the eiders shown by Johnsgard (1961a) involved an additional seven steps in the hypothesis. Similarly, the alternative placement of the Long-tailed Duck depicted by Johnsgard (1961a) required two additional steps than the phylogenetic hypothesis proposed here (Fig. 1). The tentative placement of the Labrador Duck proposed by Johnsgard (1961a) added four more steps to the hypothesis. Movement of the Smew to the position of the sister-group of *Lophodytes* and *Mergus* entailed only one additional step in the tree, whereas making the Smew the sister-group of the mergansers exclusive of *Lophodytes* necessitates an additional five steps. Finally, the topology depicted by Johnsgard (1961a) for the Common, Chinese, and Auckland Islands mergansers required an additional eight steps in the phylogeny.

Comparison with generic placements of Livezey (1986). A phylogeny presented in an earlier genus-level analysis of Anseriformes (Livezey 1986: figs. 1, 5) differed from the present hypothesis (Fig. 1) on three points. First, Livezey (1986) found that Steller's Eider and other eiders (*Somateria*) were paraphyletic to other Mergini, whereas in the present analysis the eiders are found to be monophyletic. Second, the Labrador Duck was considered to be the sister-group to the Mergini exclusive of eiders and the Harlequin Duck by Livezey (1986), whereas the Labrador Duck is hypothesized to be the sister-group of the scoters in the present analysis. The placement of the Labrador Duck must be viewed with caution, however, in light of the missing character states for this species (Appendix 2). Third, the Smew was hypothesized to be either the sister-group to the goldeneyes or to the mergansers

(including *Lophodytes*) by Livezey (1986, depicted as the former in figs. 1 and 5); in the current analysis a sister-relationship between the Smew and the goldeneyes is weakly supported as the most parsimonious hypothesis (Figs. 1, 2). Relationships inferred here (Fig. 1) among the mergansers (*Lophodytes* and *Mergus*) are identical to those presented in an earlier analysis (Livezey 1989).

Additional equally parsimonious topologies for the Mergini have been discovered through subsequent manipulations of the data set compiled by Livezey (1986) using improved versions of PAUP (J. Harshman, pers. comm.). These alternative arrangements primarily differ in (1) the depiction of the eiders, Harlequin Duck, and Labrador Duck as monophyletic and/or (2) the insertion of the monophyletic stiff-tailed ducks (Oxyurini) as the sister-group of the Mergini exclusive of the mergansers or as the sister-group of the mergansers, Smew, and goldeneyes. All of these alternatives are precluded by the enlarged data set analyzed in the present study. For example, the presence of the lobed hallux alone excludes the basal member of the Oxyurini (*Heteronetta*) from inclusion among the Mergini, and any of several new characters of the trachea, natal plumage, or definitive plumage precludes the division of the Mergini or the partitioning of the clade comprising the goldeneyes, Smew, and mergansers (Fig. 1).

EVOLUTIONARY TRENDS

The Mergini share several life-historical and ecological characters, including diving habit and primary reliance on animal prey (Weller 1964a); moderately heavy wing-loadings and rapid flight (Raikow 1973, Livezey 1993), age of sexual maturity of two or more years (Weller 1964b, Kear 1970), and predominantly diurnal activity patterns (McNeil et al. 1992). Attributes showing the clearest patterns among seaducks are (see Appendices 1, 2; not figured): primary preference for nest site (CI of character mapped onto tree *a posteriori*, 1.0), frequency of semicolonial nesting (1.0), and diving method (1.0). Several figured attributes (Fig. 3) (variation in clutch size [CI = 0.50], relative clutch mass [0.50], and sexual size dimorphism [0.5]) as well as frequency of interspecific nest parasitism (0.50; not figured) indicate moderate phylogenetic conservatism. Two other attributes having moderate phylogenetic constraint, sexual dichromatism (0.5) and migratory habit (0.5), had coincident, paraphyletic

reversals in the two southern hemisphere *Mergus* (not figured; see Appendices 1, 2). Body mass (Fig. 3) and the closely covarying egg mass (Appendices 1, 2) differed greatly among species, but this variation showed relatively low phylogenetic conservatism ($CI = 0.30$ and 0.31 , respectively). Comparatively low phylogenetic patterning is evident (Appendices 1, 2; not figured) in preferred aquatic habitat during nesting (0.40), and relative frequency of intraspecific nest parasitism (0.33) and formation of crèches (0.20).

The phylogenetic patterning of body mass among Mergini (Fig. 3) defies easy evolutionary explanation. For example, although the derived massiveness of *Somateria* presumably contributes to ease of deep diving for benthic prey (Livezey 1993), the absence of increased size in other genera having similar feeding and nesting habits (e.g., Harlequin Duck, scoters, Long-tailed Duck) remains problematic. Whatever the selective reasons for increased body size in *Somateria*, the change is most parsimoniously interpreted as a single homologous event in the common ancestor of the genus. Mean wing-loadings (g of body mass divided by cm^2 of wing area) tabulated by Livezey (1993) closely mirror these patterns in body mass. Interspecific patterns of clutch size of Anseriformes, hypothesized by Lack (1967, 1968) to be largely a reflection of energy available to females for egg production, are far from understood (Rohwer 1988). A derived reduction in clutch size in *Somateria* (Fig. 3) is established beyond question, however, and together with increased body mass in the genus manifests a substantial decrease in relative investment in eggs (Fig. 3).

At the opposite extreme are the cavity-nesting goldeneyes, Smew, and mergansers (exclusive of the aberrant southern species of *Mergus*), wherein small to medium body mass is associated with large clutch sizes, relatively massive egg production, and great sexual size dimorphism. Extremes of relative clutch mass are attained by the Bufflehead and the Hooded Merganser (Fig. 3), and extremes of sexual size dimorphism characterize the goldeneyes (Fig. 3). These findings confirm the earlier generalizations that cavity-nesting waterfowl, as well as species that have short-term pair bonds and low paternal investment in young, tend to lay large clutches and show atypically great size dimorphism (Sigurjónsdóttir 1981, Livezey and Humphrey 1984,

Scott and Clutton-Brock 1989). Increased clutch size in cavity-nesting birds is generally interpreted as a response to reduced predation (Martin 1992), but this hypothesis is not without controversy (Martin 1993). The frequency of crèche formation among Mergini is less intuitive, wherein relatively high frequency of crèches characterize both *Somateria* and the ecologically divergent clade comprising the Long-tailed Duck, goldeneyes, Smew, and mergansers (Appendices 1, 2). The occurrence of crèches and nest parasitism, at least infrequently, in most Mergini is consistent with the association between *K*-type life histories and brood amalgamation among Anatidae (Eadie et al. 1988), and the especially high frequency of nest parasitism in the goldeneyes and mergansers reflects a general increase in this parameter among cavity-nesting waterfowl (Rohwer and Freeman 1989). These reproductive characteristics, combined with ecomorphological specialization for piscivory (Woelfenden 1961, Hoerschelmann 1971, Livezey 1986), make the mergansers among the most specialized of ducks. The phylogenetic patterns in these parameters, however, indicate that at least some of this commonality is explainable by phylogeny, and the derived conditions should not be assumed to have arisen in each species independently.

BEHAVIORAL EVOLUTION AND HYBRIDIZATION

Courtship displays. Although the subject of comparatively intense study in the wild and captivity (Delacour 1959; Johnsgard 1960a, 1960b, 1961a, 1961c, 1964, 1965; Cramp and Simmons 1977), published accounts of courtship displays of Mergini do not permit the confident definition of displays of known homology and the determination of states for a sufficient number of species for formal phylogenetic analysis. Especially problematic is the inadequate information available for two especially important genera of Mergini, Harlequin Duck and Long-tailed Duck (Johnsgard 1960a), and no data whatsoever are available for the Labrador Duck or Auckland Islands Merganser. Moreover, the diversity of displays observed in the Mergini renders especially difficult the determination of homologies, even among closely related genera (Johnsgard 1963). Ethological inventories for the Mergini (Johnsgard 1960a, 1961a, 1961c, 1962, 1964,

1965), however, permit two probable tribal synapomorphies to be tentatively identified in the context of the present phylogenetic hypothesis (Fig. 1): precopulatory "upwards-stretch" by males and precopulatory preening. Several other displays show variation among the Mergini and therefore may provide additional insights into evolution within the tribe, including (Johnsgard 1960a): precopulatory drinking by males, copulatory wing-flicks, postcopulatory "rotations," and postcopulatory "steaming."

Interspecific hybridization. Hybridization among species of Mergini is rare, compared to other tribes of Anatinae, but a diversity of hybrid combinations of species and genera in the tribe has been documented, including interspecific hybridization between congeners of all polytypic genera, hybridization between members of different genera of Mergini, and hybridization between some Mergini and members of other tribes of Anatidae (Ball 1934, Gray 1958, Johnsgard 1960c, Weller 1964c, Scherer and Hilsberg 1982). Available compilations suggest that *Bucephala*, *Mergellus*, *Lophodytes*, and *Mergus* are the genera of Mergini most frequently involved in intergeneric hybridization (Ball 1934, Gray 1958, Johnsgard 1960c). Inter-tribal hybridization by Mergini most frequently involved pairings with dabbling ducks (Anatini) or pochards (Aythyini) (Johnsgard 1960c).

Frequency of interspecific hybridization traditionally has been considered an index to phylogenetic relationships among Anseriformes, and relatively high frequencies have been interpreted as the absence or failure of selectively advantageous, often behaviorally based mechanisms of species discrimination and reproductive isolation (Sibley 1957, Johnsgard 1963). An alternative, phylogenetically oriented view holds that interspecific hybridization simply reflects the retention of *primitive* reproductive compatibility among species, and therefore is not a reliable index of relationship; presumptions concerning selection for "isolating mechanisms" are irrelevant to the issue and remain poorly reasoned (Livezey 1991). It is unlikely that frequencies of hybridization will provide compelling empirical weight to either perspective, and the choice of interpretation is likely to remain one grounded in systematic philosophy. For example, the relatively high frequency of intergeneric hybridization among the goldeneyes, Smew, and the mer-

gansers is consistent with either view. However, if fertile hybrids between eiders and Harlequin Ducks were common, a phylogenetic interpretation based on the presented tree (Fig. 1) would infer that primitive interspecific infertility simply was retained (i.e., is symplesiomorphic) in the segment of the paraphyletic grade including these two genera.

BIOGEOGRAPHY

General patterns. With currently available data, a northern-hemisphere origin of the Mergini is an unavoidable inference (Howard 1964, Weller 1964d). All Mergini but two members of the most-derived clades in the tribe are limited in distribution to the northern hemisphere, and breeding by many of these is largely limited to the Holarctic. Holarctic distributions of genera and subgenera, within which species occupy largely or completely allopatric subregions, is a pattern repeated in *Somateria* (especially the *S. mollissima* complex), *Melanitta fusca*-gp., *Melanitta nigra*-gp., and *Bucephala*; this strongly suggests speciation stemming from relatively recent vicariance events. The distributional patterns of a number of seaducks (*Polysticta stelleri*, *Somateria (m.) v-nigrum*, *Somateria fischeri*, *Histrionicus histrionicus*, *Bucephala islandica*, and *Mergus squamatus*) indicate the historical importance of the Pacific basin and adjacent continental areas for speciation within the Mergini. The California distribution of the fossil seaducks of the genus *Chendytes* underscores the diversity of Mergini in the Pacific region (Livezey 1993). Two of these largely Pacific species, Harlequin Duck and Barrow's Goldeneye, also have lesser populations in another apparent historical refugium, the northern Atlantic. The Atlantic region also includes the former distributional range of the extinct Labrador Duck, as well as several of the most distinguishable populations of the *S. mollissima* complex. Both the Pacific and Atlantic refugia were probably isolated during northern glaciations (Rand 1948, Ploeger 1968).

Southern-hemisphere mergansers. The most intriguing biogeographical anomaly of the Mergini concerns the distributions of the extinct Auckland Islands and critically endangered Brazilian mergansers. Regardless of inferred phylogenetic position of these species within *Mergus* (e.g., Johnsgard 1961a; Livezey 1989, present study), the isolated distributions and unique

characteristics of these two forms pose challenging evolutionary questions. In addition to their widely separated, southern distributions, the two species are the only Mergini that are nonmigratory and lack sexual dichromatism. The Brazilian Merganser (Bartmann 1988), and possibly also the Auckland Islands Merganser (Livezey 1989), differ(ed) from other Mergini in having protracted pair bonds. Both species probably shared a specialization for riverine habitat (Livezey 1989). The absence of sexual dichromatism (Appendices 1, 2; not figured) is not homologous in the two species, however, evidently being pedomorphic in the Auckland Islands Merganser but the result of a uniquely derived, nonpaedomorphic definitive plumage in the Brazilian Merganser (Livezey 1989). The Auckland Islands Merganser is unique among *Mergus* in its high-latitude, insular habitat, although ongoing collection of subfossil remains also has documented the former presence of *M. australis* or a sister-species on the Chatham Islands and mainland New Zealand (P. Millener, pers. comm.). The positions of the two southern *Mergus* within the phylogeny of the tribe and their geographical distributions strongly suggest that each was founded independently by trans-equatorial dispersal events, and make the two species unusually well suited for the study of parallel evolutionary divergence in waif-founded populations of Anseriformes.

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APPENDIX 1

CHARACTER DESCRIPTIONS

Characters analyzed as unordered unless marked by "O"; primitive states correspond to state "a" unless another state is highlighted in boldface. CI = consistency index.

SKELETON

Numbers of characters based on Livezey (1986) are given in parentheses. Character 24 of Livezey (1986) has been determined to be unreliable and was mis-coded in the Mergini, and is deleted. Erratum of tree labelling (*not* data analysis) in Livezey (1986: Fig. 5): basal character change "78a–c" should be "75a–c."

1. Cranium, os prefrontale, processus supraorbitalis: (a) small, straight, essentially coplanar with os frontale, facies dorsalis; (b) long, slender, dorsally directed, often curved (Livezey 1986: character 11, revised). CI = 0.50.

2. Cranium, os frontale, dorsal inflation (Möller 1969a): (a) absent; (b) present. CI = 1.00. (See character 47.)

3. Maxilla, shape: (a) not markedly narrow, not specialized for piscivory (*Mergellus* somewhat intermediate); (b) narrow, specialized for piscivory. CI = 1.00.

4. Cranium, os prefrontale, processus orbitalis; distinct broadening, lateral convexity, distal rounding: (a) absent; (b) present. CI = 1.00.

5. Sternum, corpus sterni, facies visceralis sterni, foramen pneumaticum: (a) open, ovoid; (b) absent; (c) reduced, largely occluded by medial lamina (Livezey 1986: character 78, revised). CI = 0.40.

6. Sternum, rostrum sterni, spina externa: (a) long, peg-like; (b) pair of points separated by a shallow medial sulcus; (c) obsolete; (d) single, short, dorsoventrally compressed flange (Livezey 1986: character 79, revised). CI = 0.60.

7. Sternum, carina sterni, margo ventralis (lateral perspective): (a) convex throughout; (b) essentially straight (Livezey 1986: character 80). CI = 1.00.

8. Sternum, rostrum sterni, labrum dorsalis: (a) rounded notch; (b) rounded notch with small spina interna medially (Livezey 1986: character 82). CI = 1.00.

9. Sternum, corpus sterni, trabecula mediana, marked extension caudal to linea intermuscularis and processus caudolateralis: (a) absent; (b) present (Livezey 1986: character 83). CI = 1.00.

10. Sternum, corpus sterni, caudal closure of incisura medialis, forming fenestra medialis: (a) absent; (b) present (Livezey 1986: character 84). CI = 1.00.

11. Humerus, extremitas proximalis humeri, fossa pneumaticipitalis, foramen pneumaticum: (a) present, fossa largely open; (b) absent, fossa entirely closed; (c) reduced to scattered foramina pneumatica in osseous surface (Livezey 1986: character 28). CI = 0.67.

12. Humerus, extremitas proximalis humeri, crista bicipitalis, distal segment: (a) poorly developed or simply shelf-like; (b) produced medially, enclosing elongate sulcus, typically with translucent cranial wall (Livezey 1986: character 30). CI = 1.00.

13. Carpometacarpus, extremitas proximalis carpometacarpi, trochlea carpalis, labrum dorsalis, prominent swelling on distal terminus: (a) present; (b) absent (Livezey 1986: character 37, description corrected with respect to labrum involved). CI = 0.50.

14. Carpometacarpus, corpus carpometacarpi, os metacarpale majus, facies dorsalis, impressio m. extensor metacarpi ulnaris, position relative to synostosis metacarpalis proximalis: (a) opposite, at least in part; (b) completely distal (Livezey 1986: character 43, revised). CI = 1.00.

15. Femur, extremitas proximalis femoris, trochanter femoris, cranial prominence relative to that of caput femoris: (a) significantly greater; (b) approximately equal (Livezey 1986: character 52). CI = 1.00.

16. Femur, corpus femoris, craniocaudal curvature (lateral perspective): (a) essentially absent, straight; (b) moderate; (c) pronounced, subangular (Livezey 1986: character 55). CI = 0.67.

17. Femur, extremitas distalis femoris, fossa poplitea: (a) shallow; (b) deep (Livezey 1986: character 56). CI = 1.00.

18. Tibiotarsus, extremitas distalis tibiotarsi, condylus medialis, cranial prominence relative to condylus lateralis: (a) distinctly greater; (b) approximately equal (Livezey 1986: character 64). CI = 1.00.

19. Tibiotarsus, extremitas proximalis tibiotarsi, crista cnemialis cranialis, continuation by distinct ridge on corpus tibiotarsi, facies cranialis to distal terminus of crista fibularis: (a) absent; (b) present (Livezey 1986: character 65). CI = 1.00.

20. Tarsometatarsus, extremitas distalis tarsometatarsi, canalis interosseus tendineus, lamina covering dorsal of two canaliculi: (a) intact, obscuring dorsal canaliculus in dorsal view; (b) largely incomplete or absent, exposing dorsal canaliculus in dorsal view (Livezey 1986: character 69). CI = 1.00.

TRACHEA (Fig. 4)

21. Syrinx, bulla syringealis (O): (a) present, large, tympanum distinctly asymmetrical; (b) present, small,

tympanum roughly symmetrical; (c) obsolete (King 1989). CI = 1.00.

22. Syrinx, bulla syringealis, fenestrae: (a) absent; (b) present. CI = 1.00.

23. Bulla syringealis, relative to cranial margin of fused portion of trachea: (a) left side not cranially prominent; (b) left side cranially prominent. CI = 0.50.

24. Bulla syringealis: (a) not as follows; (b) cranially peaked, with two narrow arches enclosing three obliquely opposing fenestrae. CI = 1.00.

25. Bulla laryngealis: (a) absent; (b) present (Yarrell 1885, McLelland 1989); (x) not known (some type of enlargement described inadequately for *Camptorhynchus*). CI = 1.00.

26. Bulbus trachealis, single, dorsoventrally compressed and ovoid, composed of fused tracheal rings: (a) absent; (b) present (Yarrell 1885, McLelland 1989). Note.—Reported paired swellings in *Camptorhynchus*, if accurate, not considered homologous. CI = 1.00.

27. Bulbus trachealis, in which tracheal rings are not truly fused: (a) absent; (b) present. CI = 0.50.

28. Bulla syringealis, right lobe (if present): (a) relatively small; (b) markedly enlarged. CI = 1.00.

NATAL PLUMAGE (Fig. 5)

29. Pale (buffy) facial stripes: (a) absent; (b) present, narrow; (c) present, broad. CI = 1.00.

30. Pale dorsal (scapular and rump) spots: (a) present (variably reduced in *Mergellus*); (b) absent. CI = 0.33.

31. Contrasting, dark breast band: (a) absent; (b) present. CI = 0.33.

32. Breast band (if present): (a) uniform or continuously graded; (b) distinctly two-parted, darker cranially, paler caudally. CI = 1.00.

33. White suborbital spot: (a) absent; (b) present. CI = 1.00.

34. Ventrum: (a) whitish; (b) dusky. CI = 0.33.

35. Narrow, whitish loreal stripe: (a) absent; (b) typical. CI = 1.00.

36. Tawny wash on cheeks, breast: (a) absent; (b) present. CI = 1.00.

37. Buffy malar stripe: (a) absent; (b) present. CI = 1.00.

38. Pale femoral patches: (a) absent or indistinct; (b) deep, often bounded ventrally with dark, forming third pair of dorsal spots. CI = 0.50.

39. Contrasting pale cheeks: (a) absent; (b) present. CI = 1.00.

40. Color of head: (a) brown or gray, lacking reddish tones; (b) reddish brown. CI = 1.00.

41. Dark, comparatively ventrally bowed cheek stripe: (a) absent; (b) present (indistinct in *Mergus australis*). CI = 1.00.

42. Narrow, white suborbital stripe, confined ventrally by dark cheek stripe: (a) absent; (b) present. Note.—State in *M. octosetaceus* based on illustrations in Partridge (1956) and Delacour (1959), although presence not evident in photographs by Bartmann (1988). CI = 1.00.

43. Whitish antorbital spot: (a) absent; (b) present. CI = 0.50.

44. Pale alar stripe: (a) present; (b) absent. CI = 0.50.

45. Wing linings: (a) pale; (b) dark, with only a few scattered pale feathers. CI = 1.00.

DEFINITIVE PLUMAGES AND SOFT PARTS

Pertain to definitive alternate plumages of males unless indicated otherwise.

46. Iris color (especially males): (a) brown; (b) bright white; (c) yellow; (d) red. CI = 0.75.

47. Basal swelling of maxilla (also involves underlying bone; Möller 1969b): (a) absent; (b) present, predominately dorsal; (c) present, predominately lateral. CI = 1.00. (See character 2.)

48. Bill, ground color: (a) gray; (b) yellow or orange. CI = 0.33.

49. Bill color, basal (partly seasonal) intensification of greenish-yellow color (where present) to orange-red: (a) absent; (b) present, orange, especially males in breeding season (*S. spectabilis* comparatively reddish). CI = 0.50.

50. Bill color, contrasting yellow patches: (a) absent; (b) present, lateral; (c) present, medial. CI = 1.00.

51. Bill color, females: (a) lacking yellow patches; (b) with yellow patches. CI = 1.00.

52. Hallux, lobation: (a) absent; (b) present. CI = 1.00.

53. Foot color: (a) gray; (b) greenish, with variable yellow tones; (c) orange; (d) pink. CI = 0.60.

54. Conspicuously elongate maxillary cornices: (a) absent; (b) present (evident only in female of *S. spectabilis*). CI = 1.00.

55. Elongate maxillary cornices (if present) (O): (a) acuminate; (b) not distinctly broad, moderately rounded; (c) comparatively broad, rounded. CI = 1.00.

56. Black, lateroventral border of bill: (a) absent; (b) present. CI = 1.00.

57. Basal feathering on lateral surfaces of maxilla (evident also in natals) (O): (a) absent; (b) present, moderate; (c) present, extensive; (d) present, extreme, reaching narial aperture. CI = 0.50.

58. Facial pattern (females): (a) not as follows; (b) dark with separate, pale antorbital and auricular spots; (c) dark with sharply defined, pale cheek extending dorsally to just below orbit. CI = 1.00.

59. Medially divided, black crown: (a) absent; (b) present. CI = 1.00.

60. Black border anterior and ventral to orbit: (a) absent; (b) present. CI = 1.00.

61. Periorbital, narrow black border enclosing significant area of white: (a) absent; present. CI = 1.00.

62. Black chevron on throat (O): (a) absent; (b) present, rare; (c) present, typical. Note.—See Humphrey (1955) and Palmer (1976). CI = 0.67.

63. Suborbital green region: (a) absent; (b) present. CI = 1.00.

64. White, crescent-shaped, orbital patches: (a) absent; (b) present. CI = 1.00.

65. Head plumage, blackish with iridescence: (a) absent; (b) present, greenish; (c) present, bronze-green; (d) present, purplish. CI = 0.60.

66. Sharply defined, variably shaped, white antorbital spots: (a) absent; (b) present. CI = 0.50.

67. Nuchal crest: (a) absent; (b) present, uniformly long, continuously emergent from corona to occiput; (c) present, essentially one-parted tuft from corona; (d) present, shaggy, unevenly long, typically "two-parted." CI = 1.00.

68. Nuchal region: (a) not green; (b) with restricted green nuchal prominence; (c) extensively green; (d) light blue. CI = 1.00.
69. Broad, complete white collar separating largely dark head from dark mantle: (a) absent; (b) present. CI = 0.50.
70. Narrow, dark nape stripe interrupting white neck collar: (a) absent; (b) present. CI = 1.00.
71. Upper back (mantle): (a) variably colored; (b) immaculately white. CI = 1.00.
72. White of mantle (if present), extending latero-caudally, producing lateral flank patches: (a) absent; (b) present. CI = 1.00.
73. Scapulars: (a) not conspicuously elongate, shorter than underlying tertials; (b) greatly elongate, at least as long as tertials. CI = 1.00.
74. Tertials: (a) not as follows; (b) elongate, laterally curved. CI = 1.00.
75. Scapulars, contrasting lateral black stripe: (a) absent; (b) present, variably extensive. CI = 1.00.
76. Scapulars, tertials, ground color: (a) variably dark brown, gray or black; (b) white. CI = 0.50.
77. Chin, restricted white patch (adult females): (a) absent; (b) present. CI = 1.00.
78. Paired, ventrally diverging, black shoulder stripes separated by white: (a) absent; (b) present. CI = 0.50.
79. Breast, ground color: (a) dark brown; (b) white (buffy in *Polysticta*, ventrally restricted in *Somateria fischeri*, heavily barred in *Mergus octosetaceus*, suffused with pale gray in *M. australis*); (c) black(ish); (d) slate-blue; (e) red. CI = 0.60.
80. Lower breast, sides, belly: (a) not jet black; (b) jet black, like vent. CI = 0.50.
81. Sides and flanks, blackish barring or vermiculations: (a) absent; (b) present, essentially linear; (c) present, broad scalloping. CI = 0.40.
82. Flanks, crus, and lower belly (females) (O): (a) lacking contrastingly dusky suffusion; (b) dusky suffusion present on crural region, but not extending across vent between thighs; (c) dusky suffusion on crural region and extending between thighs forming trans-abdominal band. Note.—Codings for *Mergus australis*, *M. octosetaceus* difficult. CI = 1.00.
83. Typical contour feathers (females): (a) not as follows; (b) brown with black, transverse bars or horse-shoe-shaped marks. CI = 1.00.
84. Predominately blackish body plumage, dorsally, ventrally, and laterally (readily wearing to brown): (a) absent; (b) present. CI = 1.00.
85. Lesser upper wing coverts, ground color: (a) variably dark throughout; (b) white throughout; (c) dark on leading edge, white behind. CI = 0.25.
86. Conspicuous black bar across white dorsal wing region (formed by the exposure of comparatively extensive black proximal portions of greater secondary coverts by overlying white or pale gray median secondary coverts): (a) absent; (b) present. CI = 1.00.
87. Metallic, contrastingly colored secondary remiges (wing speculum): (a) present, bordered caudally with white, in both sexes; (b) vestigial, caudally bordered with white, in females, but absent in males; (c) present, but not bordered caudally with white, in males, but absent in females; (d) absent in both sexes. CI = 1.00.
88. Axillaries: (a) dark brown; (b) white. CI = 0.25.
89. Wing linings: (a) dark, or mottled with dark; (b) essentially pure white. CI = 0.50.
90. Outermost primary remiges: (a) not distinctly emarginate; (b) distinctly emarginate, especially in adult males. Note.—See Dwight (1914). CI = 1.00.
91. Secondary remiges (O): (a) dark or metallicallly toned; (b) blackish (medio)proximally, white (latero)distally; (c) entirely white. CI = 0.67.
92. Uppertail coverts (rump): (a) black; (b) gray or brown. CI = 0.50.
93. Undertail coverts (vent): (a) not uniformly colored, typically mottled brown; (b) blackish; (c) essentially white. CI = 1.00.
94. Rectrices: (a) not elongate, pointed; (b) elongate, pointed. CI = 1.00.
95. Dusky gray, spotted cranial border to white vent: (a) absent; (b) present. CI = 0.50.
96. Modal number of pairs of rectrices (O): (a) seven; (b) eight; (c) nine. CI = 0.67.
97. Head and mentum dark uniform brown, with sharp demarcation from paler color of upper breast (definitive females): (a) absent; (b) present. CI = 1.00.
98. Iridescent purple, white-striped scapulars: (a) absent; (b) present. CI = 1.00.
99. Distinct, black shoulder spots: (a) absent; (b) present. CI = 1.00.
100. Largely rufous ventrum: (a) absent; (b) present. CI = 1.00.
101. Purplish-black throat, collar: (a) absent; (b) present. CI = 1.00.
102. Fine, sharply defined, black orbital rings or "spectacles": (a) absent; (b) present. CI = 1.00.
103. Large, red crista cornea frontalis ("frontal shield"): (a) absent; (b) present. CI = 1.00.
104. Narrow, elongate, black crown stripe: (a) absent; (b) present. CI = 1.00.
105. Sharply defined, white, auricular spot: (a) absent; (b) present. CI = 1.00.
106. Narrow, white stripes on sides of neck: (a) absent; (b) present. CI = 1.00.
107. Pair of black-bordered, white stripes on shoulders: (a) absent; (b) present. CI = 1.00.
108. Small, sharply defined, white flank spots: (a) absent; (b) present. CI = 1.00.
109. Contrastingly deep chestnut sides: (a) absent; (b) present. CI = 1.00.
110. Irregular, white preorbital and circular, white postorbital spots (females): (a) absent; (b) present. CI = 1.00.
111. Head and neck (exclusive of crown) white: (a) absent; (b) present. CI = 1.00.
112. Narrow black crown patch, terminating at occiput: (a) absent; (b) present. CI = 1.00.
113. Narrow, contrastingly black collar: (a) absent; (b) present. CI = 1.00.
114. Patch of distinctly stiffened feathers on cheek: (a) absent; (b) present. CI = 1.00.
115. Distinctly spatulate bill (both sexes): (a) absent; (b) present. CI = 1.00.
116. Yellow basal bill swelling (derived extension of medial yellow patch of maxilla to include basal knob): (a) absent; (b) present. CI = 1.00.
117. Uniquely prominent basal bill swelling: (a) absent; (b) present. CI = 1.00.

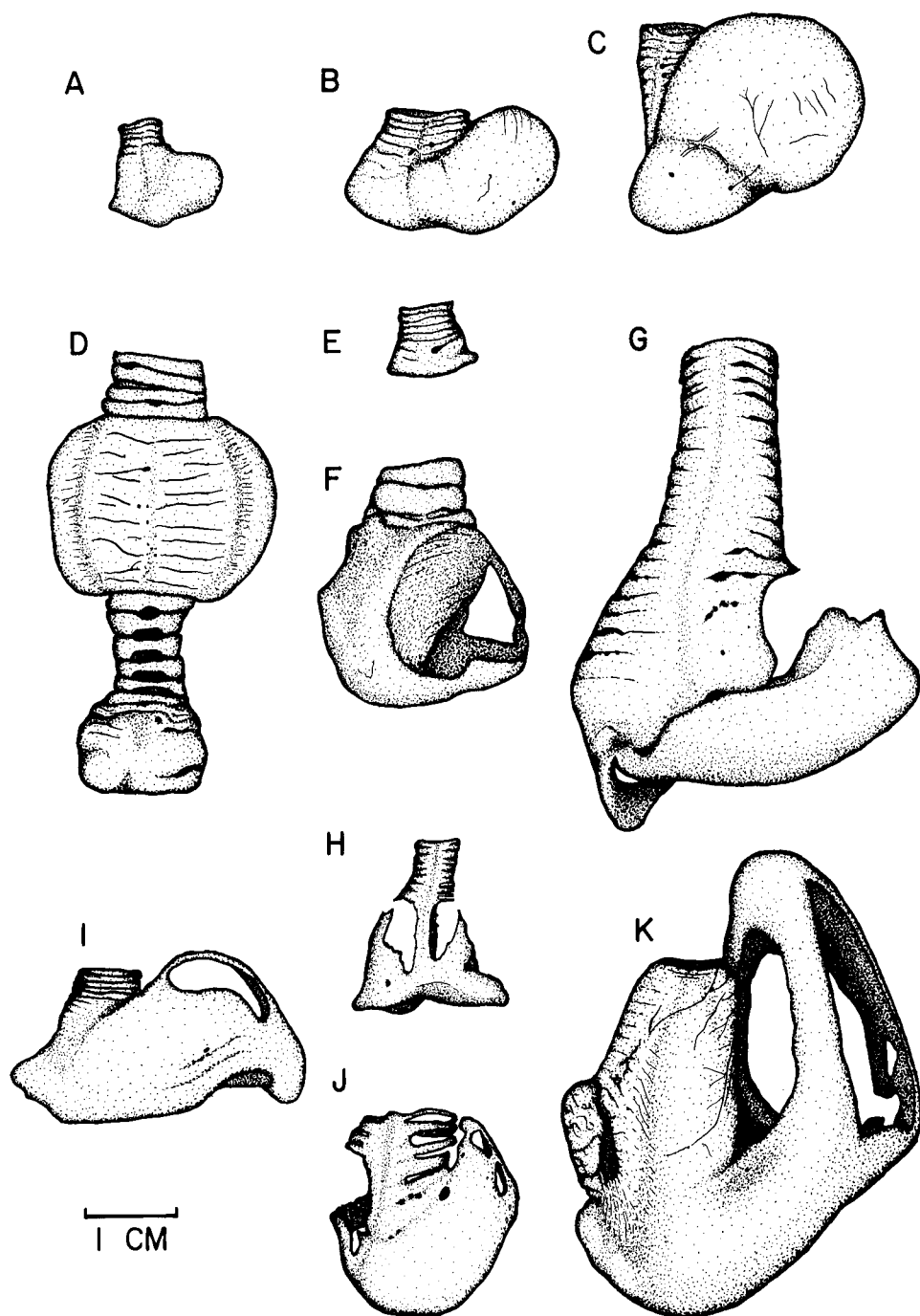


FIGURE 4. Osseous tracheal and syringeal structures of male Mergini, ventral views: A—*Polysticta stelleri*, bulla syringealis (USNM 224029); B—*Somateria (mollissima) dresseri*, bulla syringealis (KUMNH 13336); C—*Histrionicus histrionicus*, bulla syringealis (KUMNH 60514); D—*Melanitta perspicillata*, bulbus trachealis and bulla syringealis (KUMNH 31307); E—*Melanitta (nigra) americana*, tympanum syringealis (UMMZ 225126); F—*Clangula hyemalis*, bulla syringealis (USNM 499413); G—*Bucephala clangula*, bulla syringealis (FMNH 348957); H—*Bucephala albeola*, bulla syringealis (UMMZ 198362); I—*Mergellus albellus*, bulla syringealis (USNM 585082); J—*Lophodytes cucullatus*, bulla syringealis (KUMNH 13816); K—*Mergus merganser*, bulla syringealis (KUMNH 67638).

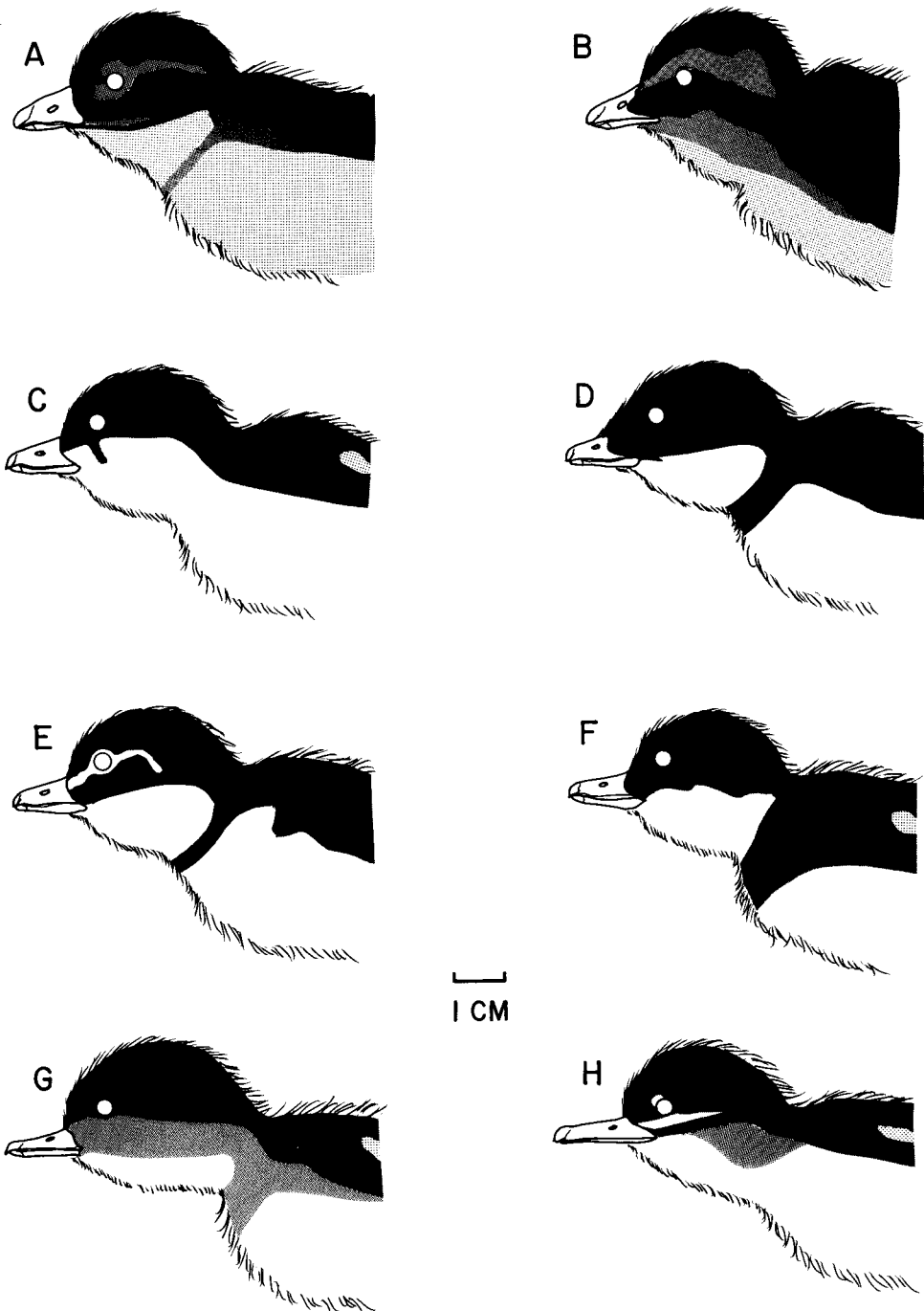


FIGURE 5. Plumage patterns of natal Mergini, lateral views: A—*Polysticta stelleri* (USNM 121267); B—*Somateria (mollissima) dresseri* (FMNH 25861); C—*Histrionicus histrionicus* (USNM 79065); D—*Melanitta (fusca) deglandi* (UMMZ 121344); E—*Clangula hyemalis* (USNM 88948); F—*Bucephala clangula* (FMNH 129623); G—*Lophodytes cucullatus* (USNM 82293); H—*Mergus serrator* (USNM 203184).

118. Contrasting, white frons and nuchal patches: (a) absent; (b) present. CI = 1.00.

119. Laterally extensive, elaborately patterned maxillar plates: (a) absent; (b) present. CI = 1.00.

120. Scapulars black medially with tawny margins (supplemental, males): (a) absent; (b) present. CI = 1.00.

121. Head and neck entirely black except for white, tear-shaped orbital patch (supplemental, males): (a) absent; (b) present. CI = 1.00.

122. Head and upper neck grayish white except for black lower cheeks (alternate, males): (a) absent; (b) present. CI = 1.00.

123. Scapulars uniformly pale, grayish white (alternate, males): (a) absent; (b) present. CI = 1.00.

124. Greatly elongated medial rectrices (all definitive plumages, males): (a) absent; (b) present. CI = 1.00.

125. Subterminal pink region on maxilla (both sexes): (a) absent; (b) present. CI = 1.00.

126. Prominent, white auriculo-nuchal patches (males, reduced in females): (a) absent; (b) present. CI = 1.00.

127. Second, more-caudal black bar in dorsal secondary coverts, caused by exposure of dark bases of secondary remiges by overlying greater secondary remiges (females): (a) absent; (b) present. CI = 1.00.

128. Sharp black shoulder marks, produced by cranioventral extensions of dark mantle: (a) absent; (b) present. CI = 1.00.

129. Head white except semicircular black orbital patch and black stripe in ventral margin of nuchal crest: (a) absent; (b) present. CI = 1.00.

130. Crown, orbital area, and nape chestnut (females): (a) absent; (b) present. CI = 1.00.

131. Sharply contrasting white throat and lower cheeks (females): (a) absent; (b) present. CI = 1.00.

132. Contrasting, pale rufous sides: (a) absent; (b) present. CI = 1.00.

133. Prominent, black-bordered, white nuchal crest: (a) absent; (b) present. CI = 1.00.

134. Ventrums densely barred with blackish (both sexes): (a) absent; (b) present. CI = 1.00.

135. Sharp black barring on breast: (a) absent; (b) present. CI = 1.00.

136. Narrow white gular stripe from breast dorsally into green collar: (a) absent; (b) present. CI = 1.00.

137. Complete, broad, white collar: (a) absent; (b) present. CI = 1.00.

ATTRIBUTES FOR MAPPING

(Primitive states are listed "a" unless given in bold.)

A. Mean body mass (unweighted mean of sexes, g; O): (a) <700; (b) 700–1,100; (c) 1,100–1,600; (d) 1,600–2,100; (e) >2,100.

B. Mean clutch size (O): (a) 4–6; (b) 6–9; (c) **9–11**.

C. Egg mass (g, after Schönwetter 1961; O): (a) <60; (b) 60–70; (c) 70–80; (d) >80.

D. Clutch mass relative to mean female body mass (O): (a) <30%; (b) 30–50%; (c) **50–70%**; (d) 70–90%; (e) >90%.

E. Age at sexual maturity (yr): (a) one; (b) two.

F. Primary nest site: (a) ground; (b) cavity.

G. Semicolonality: (a) absent; (b) typical.

H. Sexual dichromatism: (a) present; (b) absent.

I. Sexual size dimorphism (ratio of mean male mass to mean female mass, g; O): (a) <1.15; (b) 1.15–1.25; (c) >1.25.

J. Primary prey group: (a) invertebrates; (b) vertebrates.

K. Diving method: (a) wing (at least at submergence) and feet; (b) feet only.

L. Typical aquatic habitat during nesting (O): (a) freshwater; (b) freshwater and saltwater; (c) saltwater.

M. Migration: (a) present; (b) absent.

N. Formulation of crèches: (a) infrequent; (b) common.

O. Intraspecific nest parasitism: (a) infrequent; (b) common.

P. Interspecific nest parasitism: (a) infrequent; (b) common.

APPENDIX 2

CHARACTER-STATE MATRIX

This matrix of 137 morphological characters described in Appendix 1 is available from the author on request. The matrix will be supplied on diskette if a Macintosh-format diskette is provided by the reader.

APPENDIX 3

PHYLOGENETIC CLASSIFICATION

Taxonomic ranks based on inferred phylogeny (Figs. 1, 2), after the methods of Wiley (1981). Phylogenetic species recognized within traditional species taxa retain a parenthetical abbreviation of the "superspecific" taxon, and other subspecific taxa included in each follow the binomen. Note that the sequence of three generic groups *Bucephala*, *Mergellus*, and *Lophodytes* + *Mergus* is indeterminate (i.e., the sequence should be annotated *sedis mutabilis*).

ORDER ANSERIFORMES (Wagler, 1831).

Suborder Anseres Wagler, 1831.

Family Anatidae Vigors, 1825.

Subfamily Anatinae Swainson, 1837.

Tribe Mergini Delacour and Mayr, 1945.—Seaducks.

Subtribe Somaterae Boetticher, 1942.—Eiders.

Genus *Polysticta* Eyton, 1836.

Polysticta stelleri (Pallas, 1769).—Steller's Eider.

Genus *Somateria* Leach, 1819.—Greater Eiders.

Subgenus *Lampronetta* Brandt, 1847.

Somateria fischeri (Brandt, 1847).—Spec-tacled Eider.

Subgenus *Somateria* Leach, 1819.

Somateria spectabilis (Linnaeus, 1758).—King Eider.

Somateria (m.) v-nigrum Gray, 1855.—Pacific Eider.

Somateria (m.) borealis (Brehm, 1824).—Northern Eider.

Somateria (m.) dresseri Sharpe, 1871 (incl. provisionally *sedentaria* Snyder, 1941).—Canada Eider.

Somateria (m.) mollissima (Linnaeus, 1758) (incl. small, insular *faeroensis* Brehm,

1831, and provisionally *islandica* Brehm, 1831).—European Eider.
 Subtribe Mergeae Boetticher, 1942.—Typical Sea-ducks.
 Supergenous *Histrionicus* Lesson, 1828.
 Genus *Histrionicus* Lesson, 1828.
 Histrionicus histrionicus (Linnaeus, 1758).—Harlequin Duck.
 Supergenous *Melanitta* Boie, 1822.—Scoters and Labrador Duck.
 Genus *Camptorhynchus* Bonaparte, 1838.
 Camptorhynchus labradorius (Gmelin, 1789).—Labrador Duck.
 Genus *Melanitta* Boie, 1822.—Scoters.
 Subgenus *Melanitta*.—White-marked Scoters.
 Melanitta perspicillata (Linnaeus, 1758).—Surf Scoter.
 Melanitta (f.) *fusca* (Linnaeus, 1758).—Velvet Scoter.
 Melanitta (f.) *deglandi* (Bonaparte, 1814).—White-winged Scoter (incl. *stejnegeri* Ridgway, 1887).
 Subgenus *Oidemia* Fleming, 1822.—Black Scoters.
 Melanitta (n.) *nigra* (Linnaeus, 1758).—Eurasian Black Scoter.
 Melanitta (n.) *americana* (Swainson and Richardson, 1831).—American Black Scoter.
 Supergenous *Mergus*.—Linnaeus, 1758.—Mergansers and allies.
 Genus *Clangula* Leach, 1819.
 Clangula hyemalis (Linnaeus, 1758).—Long-tailed Duck.

Genus *Bucephala* Baird, 1858.—Goldeneyes.
 Subgenus *Bucephala* Baird, 1858.
 Bucephala albeola (Linnaeus, 1758).—Bufflehead.
 Subgenus *Glaucionetta* Stejneger, 1885.
 Bucephala clangula (Linnaeus, 1758).—Common Goldeneye.
 Bucephala islandica (Gmelin, 1789).—Barrow's Goldeneye.
 Genus *Mergellus* Selby, 1840.
 Mergellus albellus (Linnaeus, 1758).—Smew.
 Genus *Lophodytes* Reichenbach, 1853.
 Lophodytes cucullatus (Linnaeus, 1758).—Hooded Merganser.
 Genus *Mergus* Linnaeus, 1758.—Typical Mergansers.
 Subgenus *Promergus* Mathews and Iredale, 1913.
 Mergus australis Hombron and Jacquinot, 1841.—Auckland Islands Merganser.
 Subgenus *Prister* Heine, 1890.
 Mergus octosetaceus Vicillot, 1817.—Brazilian Merganser.
 Subgenus *Mergus* Linnaeus, 1758.—Greater Mergansers.
 Mergus merganser Linnaeus, 1758.—Common Merganser.
 Mergus serrator Linnaeus, 1758.—Red-breasted Merganser.
 Mergus squamatus Gould, 1864.—Chinese Merganser.